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ORIGINAL PAPER

Effect of salinity on the bioluminescence intensity of the heterotrophic dinoflagellates *Noctiluca scintillans* and *Polykrikos kofoidii* and the autotrophic dinoflagellate *Alexandrium mediterraneum*

Sang Ah Park[1] · Hae Jin Jeong[1,2] · Jin Hee Ok[3] · Hee Chang Kang[1] · Ji Hyun You[1] · Se Hee Eom[1] · Yeong Du Yoo[4] · Moo Joon Lee[5]

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Abstract

Many dinoflagellate species are bioluminescent, which is one of the anti-predation mechanisms in these species. In addition, dinoflagellate species experience a wide range of salinities in the ocean. However, the effects of salinity on their bioluminescence intensity has only been investigated for one species. Here, we explored the effect of salinity on the bioluminescence intensity of the heterotrophic dinoflagellate *Noctiluca scintillans* NSDJ2010 feeding on the chlorophyte *Dunaliella salina*, the heterotrophic dinoflagellate *Polykrikos kofoidii* PKJH1607 feeding on the dinoflagellate *Alexadrium minutum*, and the autotrophic dinoflagellate *Alexandrium mediterraneum* AMYS1807. Moreover, to determine the cell volume and growth effects on bioluminescence intensity, the cell volume and growth rate of three bioluminescent dinoflagellates were simultaneously investigated. The mean 200-s-integrated bioluminescence intensity (BL) per cell, equivalent to the total bioluminescence, of *N. scintillans*, *P. kofoidii*, and *A. mediterraneum* was significantly affected by salinity and increased with increasing salinity from 10 to 40. The results of the present study suggest that the total bioluminescence of *N. scintillans*, *P. kofoidii*, and *A. mediterraneum* in offshore and oceanic waters is greater than that in estuarine waters.

Keywords Bioluminescence · Dinoflagellate · Red tide · Salinity

Introduction

Bioluminescence is the production of visible light by living organisms (Wilson and Hastings 2013), and various bioluminescent organisms exist in the oceans (Shimomura 2006; Widder 2010; Wilson and Hastings 2013; Cusick and Widder 2020). Dinoflagellates are among the most common bioluminescent organisms found in the sea (Haddock et al. 2010; Cusick and Widder 2020). Bioluminescence in dinoflagellates is a defense mechanism against predators, that startle their predators or makes a predator to be seen by higher predators in darkness (Burkenroad 1943; Esaias and Curl 1972; Haddock et al. 2010; Valiadi and Iglesias-Rodriguez 2013; Prevett et al. 2019). Furthermore, the bioluminescence of dinoflagellates can lower the ingestion rate of predators (Esaias and Curl 1972; White 1979; Prevett et al. 2019). Therefore, dinoflagellate bioluminescence can affect the function of marine planktonic food webs.

Light emission from dinoflagellates is stimulated by physical stressors, such as waves, ships, submarines, fish, mammals, and zooplankton predation (Esaias and Curl 1972;

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✉ Hae Jin Jeong
hjjeong@snu.ac.kr

1 School of Earth and Environmental Sciences, College of Natural Sciences, Seoul National University, Seoul 08826, Republic of Korea

2 Research Institute of Oceanography, Seoul National University, Seoul 08826, Republic of Korea

3 Department of Marine Sciences and Convergent Engineering, College of Marine Sciences and Convergence Engineering, Hanyang University ERICA, Ansan 15588, Korea

4 Department of Oceanography, College of Ocean Sciences, Kunsan National University, Kunsan 54150, Republic of Korea

5 Department of Marine Biotechnology, Anyang University, Incheon 23038, Republic of Korea

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Morin 1983; Rohr et al. 1998; Latz et al. 2004, 2008; Maldonado and Latz 2007; Cusick and Widder 2014). Many bioluminescent dinoflagellates form red tides and harmful algal blooms (Anderson et al. 2012; Cusick and Widder 2020; Jeong et al. 2021). Dinoflagellate bioluminescence is sometimes observed as a night-time optical phenomenon during a dinoflagellate bloom (Seliger et al. 1970; Seliger 1989; Wilson and Hastings 2013; Martínez et al. 2016; Rodríguez 2020; Domingues 2021; Detoni et al. 2023). Consequently, the movements of ships and submarines can be detected from the air at night, which affects military operations (Lynch 1978, 1981; Lapota 2003, 2005; Moline et al. 2005; Haddock et al. 2010).

Total bioluminescence intensity (TBI) of dinoflagellates is known to be affected by several biological, physical, and chemical factors. For example, prey species and its density (Buskey et al. 1992, 1994; Buskey 1995; Latz and Jeong 1996), water temperature (Sweeney 1981; Jess 1985; Park et al. 2024), and light intensity in daytime affect TBI (Buskey et al. 1992; Li et al. 1996). Dinoflagellates usually experience a wide salinity range, which may affect TBI. However, prior to the present study, the effects of salinity on TBI of only one dinoflagellate, *Pyrocystis lunula*, were explored (Craig et al. 2003).

Among the dinoflagellate species, the heterotrophic dinoflagellate *Noctiluca scintillans* is known to produce the highest bioluminescence intensity, except for *Pyrocystis noctiluca* (Sweeney 1971; Buskey et al. 1992; Cusick and Widder 2014). This dinoflagellate is able to feed on diverse prey species, such as bacteria, phytoplankton, mixoplankton, and eggs of metazoans (Buskey 1995; Kirchner et al. 1996; Quevedo et al. 1999; Drits et al. 2013; Zhang et al. 2016; Stauffer et al. 2017) and often blooms in the global ocean (Anantharaman et al. 2010; Harrison et al. 2011; Lotliker et al. 2018; Valiadi et al. 2019; Jeong et al. 2021). Red tide patches of *N. scintillans* sometimes extend hundreds of kilometers in coastal and oceanic waters (Mohanty et al. 2007; Kopuz et al. 2014; Qi et al. 2019). The patches appear as long red or pink patches due to the digestion of prey during the daytime, but they emit a glowing blue light at night (Huang and Qi 1997; Padmakumar et al. 2010; Temnykh et al. 2022). Another heterotrophic dinoflagellate *Polykrikos kofoidii* has a bioluminescent capability and is able to feed on diverse dinoflagellate species (Buskey et al. 1992; Matsuyama et al. 1999; Matsuoka et al. 2000; Jeong et al. 2001, 2003, 2010; Kang et al. 2018, 2023; Kim et al. 2019). This dinoflagellate is commonly observed in coastal waters of many countries**,** particularly in Australia, Denmark, Kingdom of the Netherlands, Japan, Norway, United Kingdom, United States, Republic of Korea, Republic of South Africa, and Tanzania (Buskey et al. 1992; Matsuoka et al. 2000; Gómez 2003; Ocean Survey 20/20 2013; Tillmann and Hoppenrath 2013; Lim et al. 2017; Prabowo and Agusti 2019; OBIS 2023) Recently, the bioluminescence capability of the autotrophic dinoflagellate *Alexandrium mediterraneum* has been reported (Park et al. 2021); this species is found in the coastal waters of Greece, Italy, Spain, and Korea (John et al. 2003; Lilly et al. 2007; Penna et al. 2008; Aguilera-Belmonte et al. 2011; Giulietti 2017; Park et al. 2021). These three dinoflagellates have been found in a wide range of salinities (Elbrächter and Qi 1998; Matsuoka et al. 2000; Mohamed and Mesaad 2007; Harrison et al. 2011; Chuenniyom et al. 2012; Lim et al. 2017; OBIS 2023). Therefore, to understand bioluminescence in seas, it is necessary to explore whether the bioluminescence intensity of these dinoflagellates is affected by salinity.

In the present study, the bioluminescence intensities of *N. scintillans*, *P. kofoidii*, and *A. mediterraneum* were determined as a function of salinity. Moreover, the relationships between their bioluminescence intensity and cell volume and growth rate were investigated. The effects of cell volume of these dinoflagellates were investigated at same salinity, and the equations of linear regression between cell volume and bioluminescence intensity were determined. These results provide a basis for understanding salinity effects on the bioluminescence of heterotrophic and autotrophic dinoflagellates, as well as dinoflagellate bioluminescence in the sea.

Materials and methods

Preparation of experimental organisms

Cells of *Noctiluca scintillans* NSDJ2010*, Polykrikos kofoidii* PKJH1607, and *Alexandrium mediterraneum* AMYS1807 were isolated from water samples collected from Dangjin, Jangheung, and Yeosu, Korea, and a clonal culture of each dinoflagellate species was established (Table 1). The cultures of *N. scintillans* and *P. kofoidii* were fed with the chlorophyte *Dunaliella salina* and dinoflagellate *Alexandrium minutum* as prey, respectively. A dense culture of *N. scintillans* (approximately 5–10 cells mL^{-1}) was transferred to a 250-mL flask (Falcon; Corning Inc., NewYork, USA) that contained *D. salina* (approximately 10,000 cells mL^{-1}). In addition, a dense culture of *P. kofoidii* (approximately 50–70 cells mL^{-1}) was transferred to a 250-mL flask containing *A. minutum* (approximately 2,000 cells mL^{-1}). The *N. scintillans* and *P. kofoidii* cultures were incubated under 20 µmol photons m^{-2} s^{-1} of light-emitting diode (LED; FS-075MU, 6500 K; Suram Inc., Suwon, Korea) and 14: 10 h light: dark cycle. The *A. mediterraneum* culture was grown in F/2 seawater medium without silicate (hereafter F/2; Guillard and Ryther 1962) and was incubated under 100 µmol photons m^{-2} s^{-1} of LED and 14: 10 h light: dark cycle. The cultures of all three bioluminescent dinoflagellates and their prey species were incubated at 20℃ and a salinity of 30.

Table 1 The strain name, isolated information, and maintenance conditions of the bioluminescent dinoflagellates

Organisms	Strain name	Strain isolation information				Media/Prey for maintenance
		Collection location	Date	T	S	
Bioluminescent species						
Noctiluca scintillans	NSDJ2010	Dangjin, Korea	Oct. 2020	19.5	28.8	*Ds*
Polykrikos kofoidii	PKJH1607	Jangheung, Korea	Jul. 2016	23.6	26.4	*Am*
Alexandrium mediterraneum	AMYS1807	Yeosu, Korea	Jul. 2018	24.2	30.0	F/2
Prey species						
Dunaliella salina	DSJH1710	Jinhae, Korea	Oct. 2017	21.6	32.5	F/2
Alexandrium minutum	CCMP1888	Laguna obidos, Portugal	–	–	–	L1

T water temperature (°C), *S* salinity, *Ds Dunaliella salina, Am Alexandrium minutum*

Experimental setup

Experiments 1–3 were designed to investigate the effects of salinity on the bioluminescence intensities of *N. scintillans*, *P. kofoidii*, and *A. mediterraneum*. For each target salinity experiment, only filtered seawater or culture media containing the target salinity was used. The target salinity of seawater or culture medium was established by diluting natural seawater with deionized water or by adding sea salt to natural seawater, which has a salinity of 30. Salinity was measured using a YSI MultiLab 4010-3W (YSI, Yellow Springs, OH, United States). The flasks containing each bioluminescent species and their prey species were incubated under constant conditions or gradually transitioned to the target salinity for nine days to avoid any shock that may occur when a large change in the incubation condition occurs rapidly (Fig. S1). All of the cultures in experiments 1–3 were conducted in a culture chamber at 20 ℃. During the pre-incubation period, a 5-mL aliquot was pipetted from each flask at 2-day intervals and fixed with Lugol's solution and then the abundance of each species was determined. In all cultures, the mobility and morphology of cells were examined under a light microscope every other day to determine the amount of cell death. If almost bioluminescent dinoflagellate cells in the flask were dead by increasing or decreasing salinity, the experiments under the target salinity were not conducted.

For experiment 1, dense *N. scintillans* cultures were transferred to eight 250-mL flasks containing *D. salina* and filtered seawater. A dense culture of *D. salina* was transferred to eight flasks containing F/2 medium. During the pre-incubation period, cells of *N. scintillans* at a salinity of 30 were subsequently transferred to flasks at final salinities of 25, 20, 15, 10, and 5 by dilution. In contrast, cells of *N. scintillans* at a salinity of 30 were transferred to flasks with final salinities of 35 and 40 by the addition of salts. Almost all cells of *N. scintillans* in the flask did not survive at a salinity of 5; therefore, the experiments were conducted at salinities of 10, 15, 20, 25, 30, 35, and 40. The bioluminescence intensity and growth rate of *N. scintillans* at each target salinity were measured using the method described by Park et al. (2024). After pre-incubation, three 1-mL aliquots were taken from each flask, and the density of each experimental species was determined using a light microscope (Olympus BX51; Olympus Co., Tokyo, Japan) at a magnification of 40–200×. When prey cells in the *N. scintillans* culture were undetectable, the initial concentrations of *N. scintillans* and *D. salina* were achieved by adding a predetermined volume of culture having a known cell density to each well of the experimental well plate (Table 2). Triplicate experimental wells (mixtures of *N. scintillans* and *D. salina*), triplicate prey control wells (*D. salina* only), and triplicate predator control wells (*N. scintillans* only) were set up in 6-well culture plates (Fig. 1). One milliliter of the

Table 2 Experimental design

Expt No	BL Species	Tested salinity	BL species concentration (cells mL^{-1})	Prey concentration (cells mL^{-1})
1	*Noctiluca scintillans*	10, 15, 20, 25, 30, 35, 40	6, 5, 7, 5, 4, 7, 6	52,063, 52,458, 62,532, 68,675, 60,619, 61,032, 59,885
2	*Polykrikos kofoidii*	10, 15, 20, 25, 30, 35, 40	14, 17, 12, 16, 13, 9, 13	6230, 6491, 6468, 7068, 6343, 6993, 6838
3	*Alexandrium mediterraneum*	19, 23, 25, 30, 35, 37, 40	884, 923, 816, 897, 882, 980, 951	–

Expt No. experiment number, *BL* bioluminescence

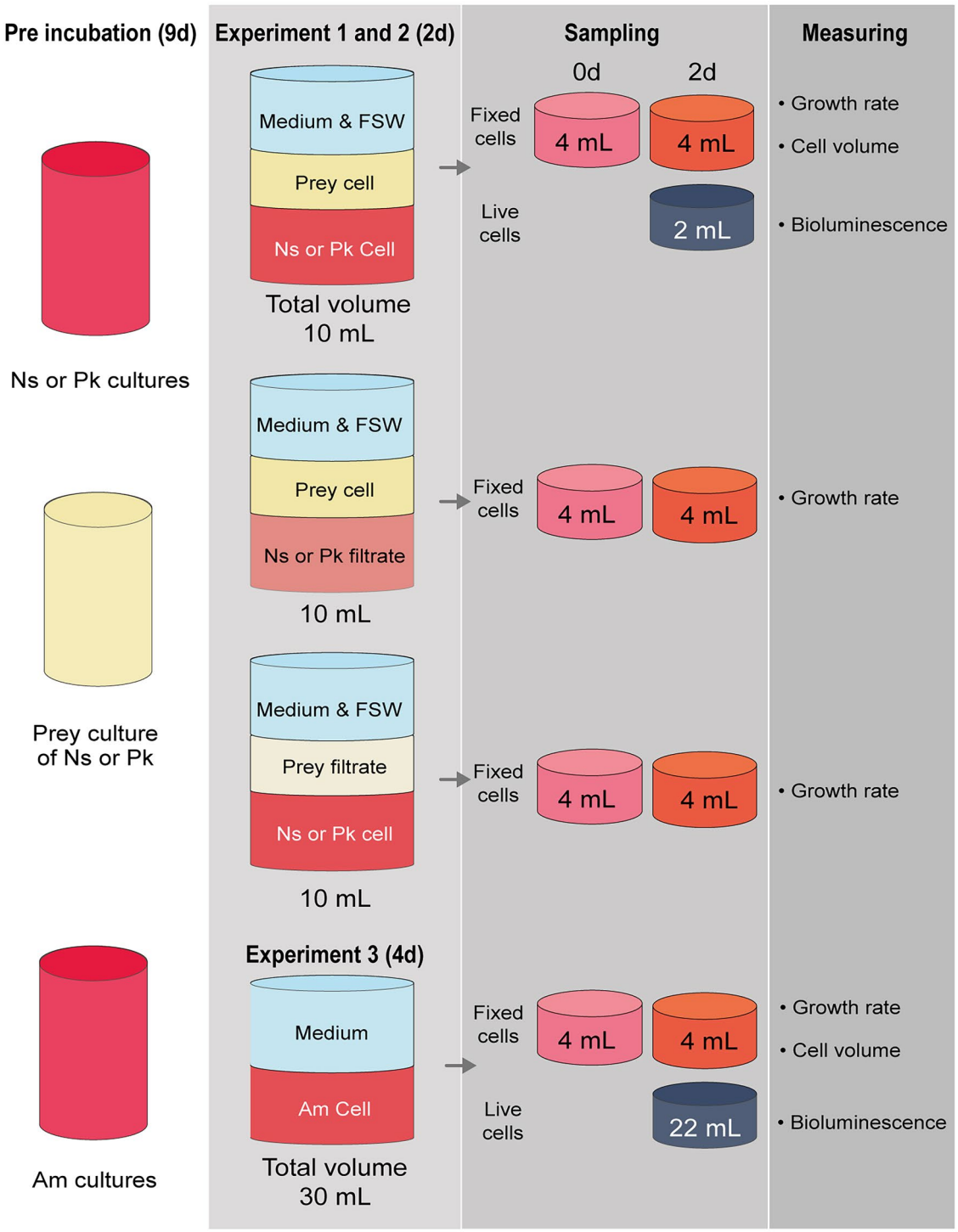


Fig. 1 Schematic diagram of the experimental procedure of this study. All the medium (F/2 or L1), filtered seawater (FSW), and cultures of *Noctiluca scintillans* (Ns), *Polykrikos kofoidii* (Pk), *Alexandrium mediterraneum* (Am), and the prey species of Ns and Pk were adjusted to the target salinity

F/2 medium at each target salinity was added to each well for each target salinity. A culture of *N. scintillans* with each target salinity was filtered with a 0.2-μm disposable syringe filter (DISMIC-25CS type, 25 mm; Advantec, Toyo Roshi Kaisha Ltd., Chiba, Japan), and then the filtrates were added to the prey control well at the same volume as that of the predator culture added to the experiment well. A culture of *D. salina* with each target salinity was filtered with a 0.2-μm

disposable syringe filter, and then the filtrates were added to the predator control well at the same volume as that of the prey culture added to the experiment well. The final volume of each well was 10 mL. These plates were incubated for two days at 20 µmol photons m^{-2} s^{-1} produced by LED lights with a cycle of 14: 10 h light: dark cycle. At the beginning and end of the experiments, 4-mL aliquots were removed from each well and fixed with Lugol's solution with a final concentration of 5%, respectively, and the densities were determined. After a 2-day incubation, the bioluminescence intensity, growth rate, and cell volume of *N. scintillans* were determined as described in the "Measurement of bioluminescence intensity" and "Measurements of the growth rate and cell volume" sections.

For experiment 2, dense *P. kofoidii* cultures were transferred to eight 250-mL flasks containing *A. minutum* and filtered seawater. *Alexandrium minutum* cells were transferred to eight flasks containing L1 medium (L1 without silicate; Guillard and Hargraves 1993). After screening the salinity by pre-incubation, the target salinities of 10, 15, 20, 25, 30, 35, and 40 were established. The procedures for establishment, incubation, and enumeration in this experiment were the same as those in Experiment 1, except for the target and prey species and culture medium (L1 without silicate instead of F/2).

For experiment 3, eight flasks were prepared and filled with fresh F/2 medium and *A. mediterraneum* cells. After screening the salinity by pre-incubation, target salinities of 19, 23, 25, 30, 35, 37, and 40 were established. By adding a predetermined volume of culture to 38-mL flask and filled with F/2 medium that adjust to each target salinity (final volume = 30 mL), the initial concentrations of *A. mediterraneum* were achieved. Culture flasks were established in triplicate at each target salinity. These flasks were incubated for four days at 100 µmol photons m^{-2} s^{-1} produced by LED lights with a cycle of 14:10 h light: dark cycle. Four-mL aliquots were removed from each flask at the beginning and end of the experiments and fixed with Lugol's solution. After a 4-day incubation, the bioluminescence intensity, growth rate, and cell volume of *A. mediterraneum* were determined.

Measurement of bioluminescence intensity

The bioluminescence intensity in each experiment was measured using the methods described by Park et al. (2021, 2024). In experiments 1 and 2, after 2-day incubation, a 200-µL aliquot of filtered seawater in each 6-well experimental plate was pipetted into a 96-well white plate (Corning Life Sciences, Amsterdam, Netherlands). Next, three cells of *N. scintillans* (or *P. kofoidii*) in each well with the target salinity were transferred to the wells of the 96-well white plate. Five replicate wells containing 3 *N. scintillans* (or *P. kofoidii*) cells and five replicate wells containing only freshly filtered seawater were established. The 96-well white plates were placed in the darkness for 3 h at 20 ℃ (Biggley et al. 1969; Krasnow et al. 1980; Lindström et al. 2017). Bioluminescence of the target dinoflagellate was stimulated chemically by adding 50 µL of 1 M acetic acid to the well of the 96-well white plate (Hastings and Sweeney 1957; Fogel and Hastings 1972; Sweeney 1986). Using a GloMax Navigator microplate luminometer (Promega, Madison, WI, USA), stimulated bioluminescence was measured for 200 s. In the experiment 3, a 200-µL aliquot of a culture of *A. mediterraneum* in each flask that was incubated for 4 days at the target salinity was placed in a well of a 96-well white plate. Five replicate wells in 96-well white plates were used. The bioluminescence intensity was measured as described above.

The bioluminescence intensity per cell per second in each well of a 96-well white plate was determined by subtracting the mean value of the bioluminescence intensity per second in the five control wells (without dinoflagellate cells) from the bioluminescence intensity value per second in each experimental well (with dinoflagellate cells) and then dividing the value by the number of cells in the experimental well. The bioluminescence intensity per cell per second for 200 s in each well was determined and the integrated bioluminescence intensity per cell for 200 s (BL per cell) was calculated. The value of BL per cell is almost equivalent to the total bioluminescence intensity per cell or the total luminescence capacity per cell (von Dassow and Latz 2002) because almost all dinoflagellate cells did not emit bioluminescence after 200 s. The mean bioluminescence intensity per cell for 200 s [mean BL per cell; relative light unit (RLU) $cell^{-1}$] was calculated by averaging BL per cell in five wells.

Measurements of the growth rate and cell volume

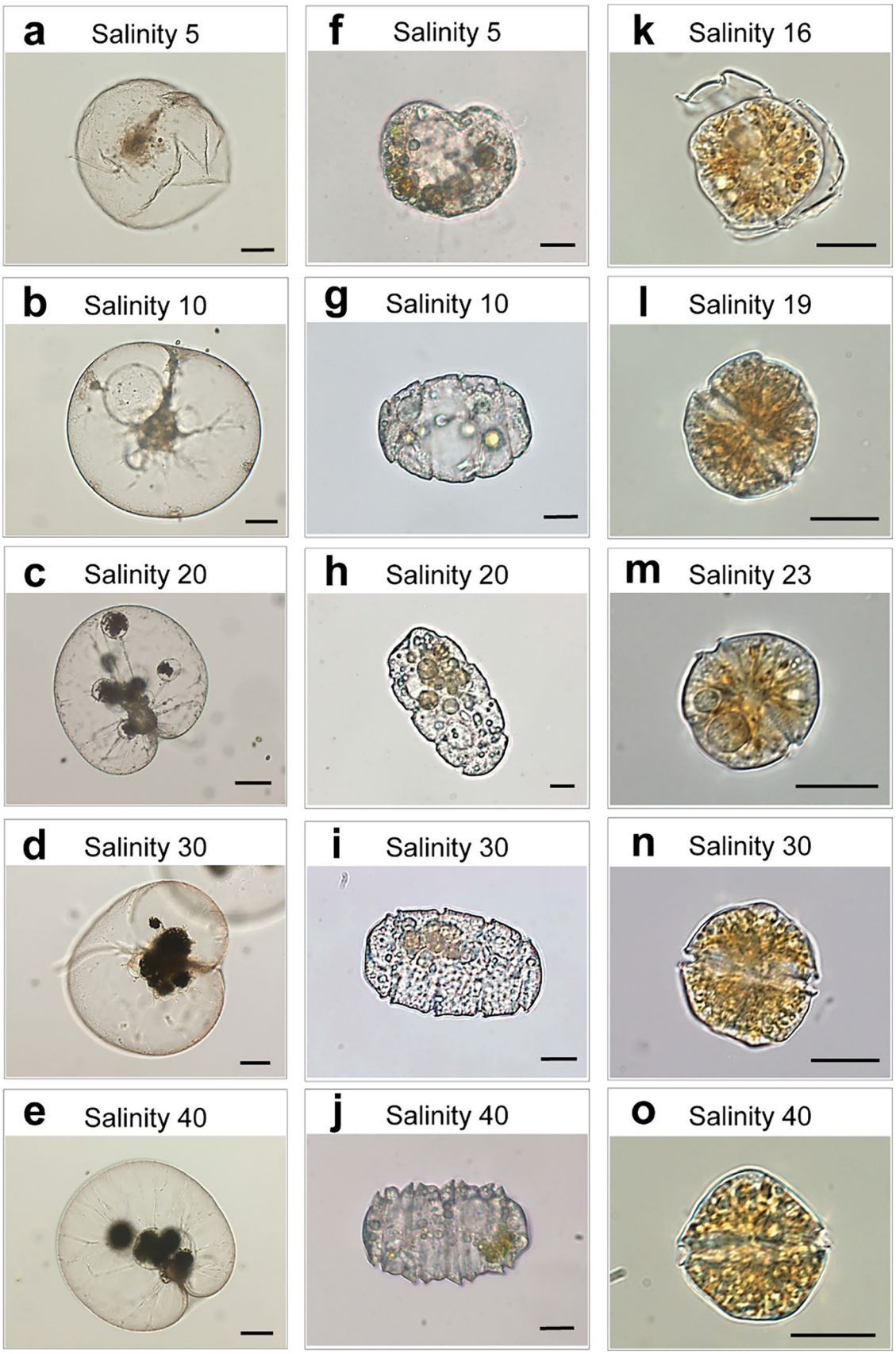
After homogenizing the cells in each well to determine the cell densities at the beginning and end of the experiments, 4-mL aliquots were taken from each well or flask and fixed with Lugol's solution at a final concentration of 5%. All or > 200 cells of a bioluminescent dinoflagellate and prey were enumerated in a Sedgewick-Rafter counting chamber (Jeong et al. 2001).

The specific growth rate of each target dinoflagellate, µ (d^{-1}), was calculated as follows:

$$\mu\left(d^{-1}\right) = [\mathrm{Ln}(C_t/C_0)]/t,$$

where C_0 and C_t are the concentrations of each target dinoflagellate at 0 and 48 h for *N. scintillans* and *P. kofoidii* or at 0 and 96 h for *A. mediterraneum*, respectively.

The cell length and width of *N. scintillans*, *P. kofoidii*, and *A. mediterraneum* preserved in 5% Lugol's solution at the end of each experiment were measured by 20 cells on a confocal dish with cover glasses using a digital camera


a Salinity 5
f Salinity 5
k Salinity 16
b Salinity 10
g Salinity 10
l Salinity 19
c Salinity 20
h Salinity 20
m Salinity 23
d Salinity 30
i Salinity 30
n Salinity 30
e Salinity 40
j Salinity 40
o Salinity 40

◂**Fig. 2** Light micrographs of cells of *Noctiluca scintillans* (**a**–**e**) and *Polykrikos kofoidii* (**f**–**j**) that were incubated for 2 days and cells of *Alexandrium mediterraneum* (**k**–**o**) that were incubated for 4 days at target salinity. Scale bars represent 100 µm (**a**–**e**), and 20 µm (**f**–**o**)

(Zeiss AxioCam 506; Carl Zeiss Ltd., Göttingen, Germany). The cell volumes of the three bioluminescent dinoflagellates were estimated to be spherical for *N. scintillans* and *A. mediterraneum* and cylindrical for *P. kofoidii*.

Statistical analyses

To examine the effect of salinity on the bioluminescence intensity of each target bioluminescent dinoflagellate, a one-way analysis of variance (ANOVA) with post-hoc Tukey's honest significant difference (HSD) test was performed (Tukey 1949). Normality was tested using Shapiro–Wilk's *W*, and homogeneity of variance was tested using Levene's tests. If the data were not normally distributed, they were analyzed using the Kruskal–Wallis test and the Mann–Whitney U test with Bonferroni correction ($P < 0.05$; Mann and Whitney 1947; Kruskal and Wallis 1952). Correlations among bioluminescence intensity, salinity, growth rate, and cell volume in each experiment were examined using the Pearson correlation coefficient or non-parametric Spearman's rank correlation coefficient. Before applying the statistical tests, using the Shapiro–Wilk *W* test, the normality of the data was confirmed. Using the SPSS ver. 25.0 (IBM-SPSS Inc., Armonk, NY, USA), statistical analyses were performed.

Results

Cell shape, cell volume, and growth rates of the dinoflagellates at different salinities

Salinities of 5–40 affected the cell shape of *N. scintillans* NSDJ2010, *P. kofoidii* PKJH1607, and *A. mediterraneum* AMYS1807 (Fig. 2). Cells of *N. scintillans* and *P. kofoidii* burst at a salinity of 5, whereas *A. mediterraneum* cells burst at a salinity of 16. Cells of *N. scintillans* and *P. kofoidii* at a salinity of 10 swelled. However, at other salinities, *N. scintillans*, *P. kofoidii*, and *A. mediterraneum* maintained their normal cell shapes.

The range of cell volumes of *N. scintillans* was $4.56–9.05 \times 10^7$ µm^3 (Fig. 3a). The cell volume of *N. scintillans* was largest at a salinity of 10 and rapidly decreased at a salinity of 15. However, there was no further decrease in the cell volume from a salinity of 15 to 40. The statistical analysis revealed no significant correlation between the cell volume of *N. scintillans* and salinity (Spearman's rank correlation coefficient, $rs = -0.10$, $P = 0.24$). The maximum cell volume of *P. kofoidii* was 3.46×10^5 µm^3 at a salinity of 10, and it gradually decreased to 1.53×10^5 µm^3 at a salinity of 35 (Fig. 3b). The cell volume of *P. kofoidii* was significantly correlated with salinity (Spearman's rank correlation coefficient, $rs = -0.62$, $P < 0.01$). The range of cell volumes of *A. mediterraneum* was $2.11–2.70 \times 10^4$ µm^3, reaching a maximum at a salinity of 19 (Fig. 3c). The cell volume of *A. mediterraneum* significantly decreased as the salinity increased (Spearman's rank correlation coefficient, $rs = -0.20$, $P = 0.02$).

The specific growth rates of *N. scintillans* feeding on *D. salina* at salinities of 10 and 40 were almost zero (-0.01 d^{-1} and 0.08 d^{-1}, respectively), whereas those at the other salinities were 0.39–0.57 d^{-1}, with the maximum growth rate at a salinity of 30 (Fig. 3d). The specific growth rate of *P. kofoidii* feeding on *A. minutum* at a salinity of 10 was almost zero (-0.04 d^{-1}), whereas the growth rates at other salinities were 0.19–0.68 d^{-1}, with the maximum growth rate at a salinity of 20 (Fig. 3e). The specific growth rate of *A. mediterraneum* at a salinity of 19 was almost zero (-0.05 d^{-1}), whereas the growth rates at the other salinities were 0.13–0.34 d^{-1}, with the maximum growth rate at a salinity of 30 (Fig. 3f). The ranges of growth rates of *D. salina* and *A. minutum* at salinities of 10 – 40 were 0.04–0.35 d^{-1} and -0.02–0.26 d^{-1}, respectively (Fig. S2).

Correlations between the growth rate and cell volume of the dinoflagellates

The growth rates of *N. scintillans*, *P. kofoidii*, and *A. mediterraneum* were not significantly correlated with their cell volumes (Fig. 4; Pearson's correlation; $r = -0.71$, $P = 0.07$ for *N. scintillans*; $r = -0.30$, $P = 0.51$ for *P. kofoidii*; $r = -0.53$, $P = 0.23$ for *A. mediterraneum*). The cell volumes of the three dinoflagellates reached a maximum when their growth rates were negative.

Effects of salinity on the bioluminescent intensity of *Noctiluca scintillans*

The mean BL per cell values of *N. scintillans* feeding on *D. salina* were significantly affected by salinity (Kruskal–Wallis test; $H6 = 23.56$, $P < 0.01$). The mean BL per cell of *N. scintillans* ranged from 0.45×10^7 to 2.78×10^7 RLU cell^{-1}, reaching a maximum at a salinity of 40 (Fig. 5). The values were divided into two subsets (Mann–Whitney U test with Bonferroni correction, $P < 0.05$). Significant positive correlations were seen between mean BL per cell of *N. scintillans* and salinity (Pearson's correlation; $r = 0.77$, $P < 0.001$).

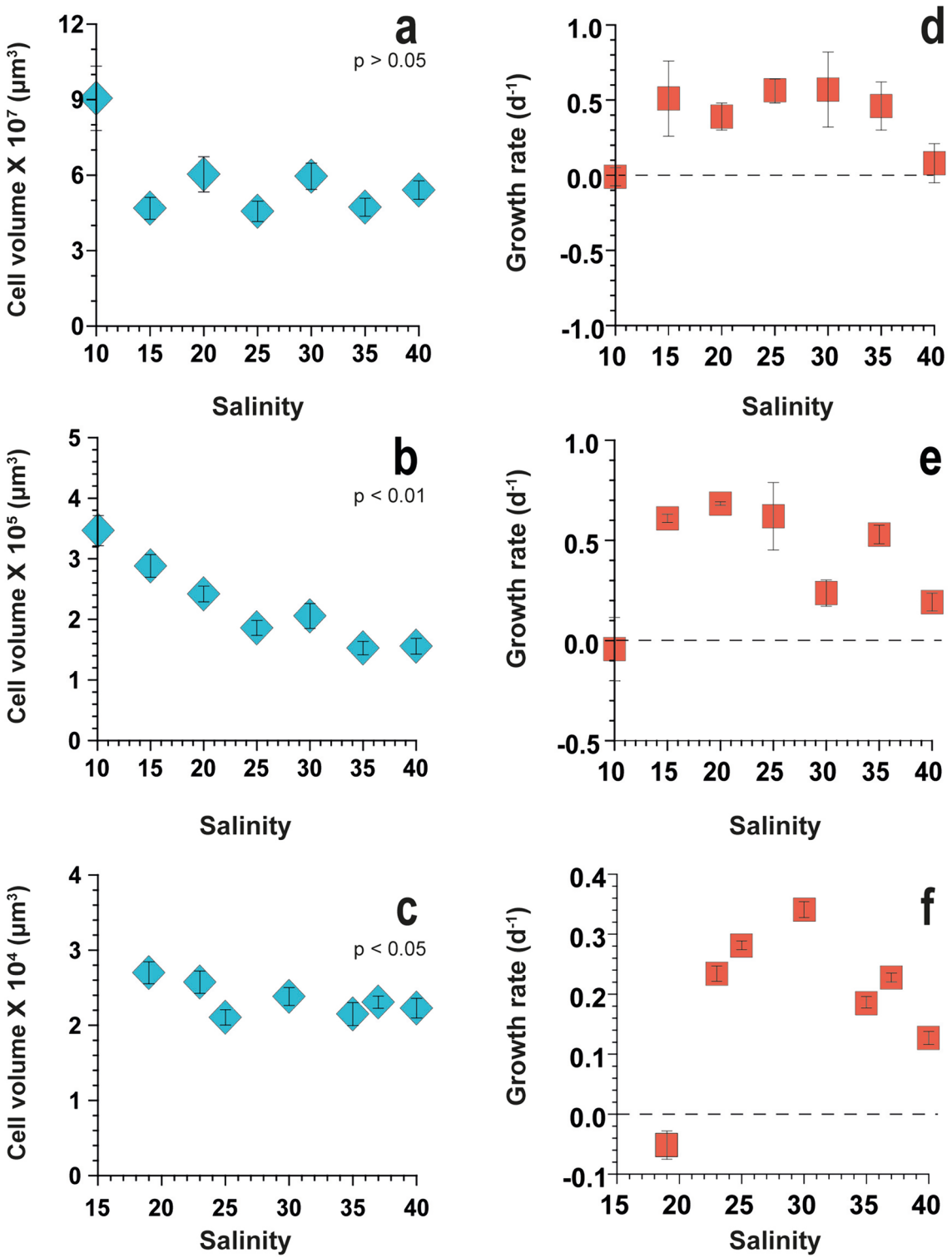


Fig. 3 Cell volume of *Noctiluca scintillans* feeding on *Dunaliella salina* (**a**) and *Polykrikos kofoidii* feeding on *Alexandrium minutum* (**b**) and *Alexandrium mediterraneum* (**c**) as a function of the salinity range. Specific growth rates of *N. scintillans* feeding on *D. salina* (**d**) and *P. kofoidii* feeding on *A. minutum* (**e**) and *A. mediterraneum* (**f**) as a function of the salinity range. Symbols represent treatment means ± standard error

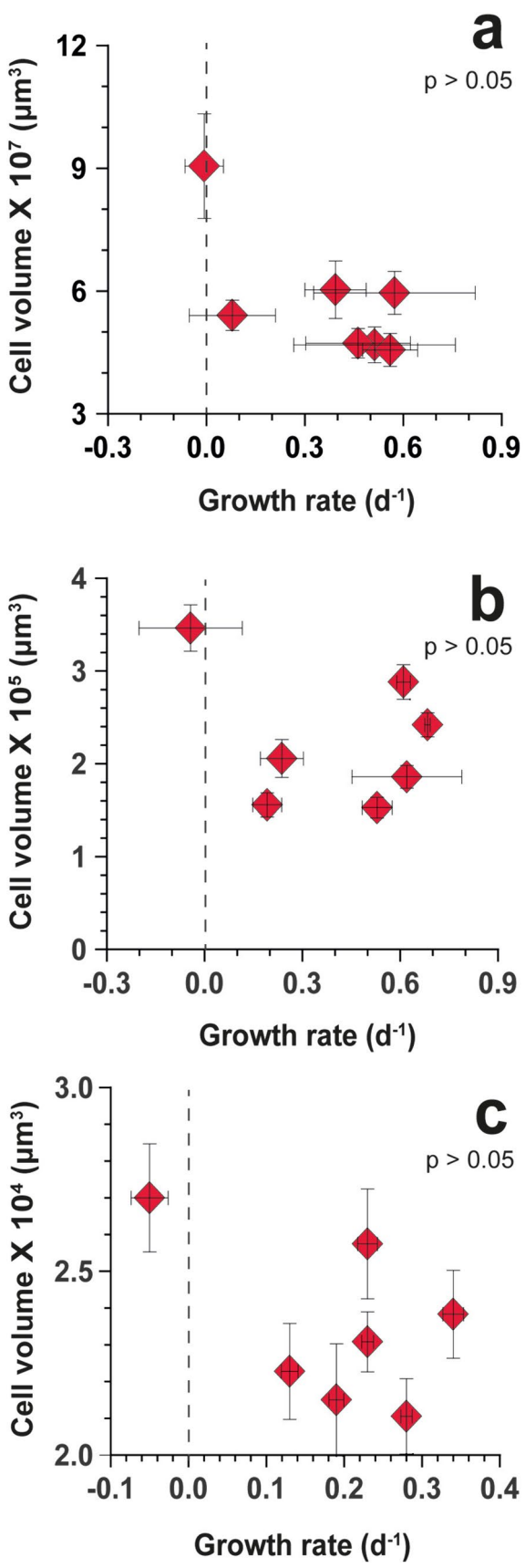


Fig. 4 Cell volume of *Noctiluca scintillans* feeding on *Dunaliella salina* (**a**) and *Polykrikos kofoidii* feeding on *Alexandrium minutum* (**b**) and *Alexandrium mediterraneum* (**c**) as a function of the growth rate of *N. scintillans*, *P. kofoidii*, and *A. mediterraneum*, respectively. Symbols represent treatment means ± standard error

Effects of salinity on the bioluminescent intensity of *Polykrikos kofoidii*

The mean BL per cell values of *P. kofoidii* feeding on *A. minutum* were significantly affected by salinity (Kruskal–Wallis test, $H6 = 25.1$, $P < 0.001$). The mean BL per cell of *P. kofoidii* at salinity 10–40 ranged from 0.31×10^5 to 3.40×10^5 RLU cell^{-1}, reaching a maximum at a salinity of 40 (Fig. 6). Bonferroni correction ($P < 0.05$) revealed that mean BL per cell values of *P. kofoidii* were divided into three subsets. Significant positive correlations were seen between mean BL per cell of *P. kofoidii* and salinity (Pearson's correlation: $r = 0.86$, $P < 0.001$).

Effects of salinity on the bioluminescent intensity of *Alexandrium mediterraneum*

The mean BL per cell values of *A. mediterraneum* were significantly affected by salinity (Fig. 7; Kruskal–Wallis test, $H6 = 22.42$, $P < 0.01$). The mean BL per cell of *A. mediterraneum* at 19–40 ranged from 0.83×10^4 to 4.49×10^4 RLU cell^{-1}, reaching a maximum at a salinity of 40. The values were divided into two subsets (Mann–Whitney U test with Bonferroni correction, $P < 0.05$). Significant positive correlations were seen between mean BL per cell of *A. mediterraneum* and salinity (Spearman's rank correlation; $rs = 0.64$, $P < 0.001$).

Correlations between the growth rate and bioluminescence intensity of the dinoflagellates

The mean BL per cell was not significantly correlated with the growth of *N. scintillans*, *P. kofoidii*, or *A. mediterraneum* (Fig. 8; Pearson's correlation; $r = -0.34$, $P = 0.46$ for *N. scintillans*; $r = -0.11$, $P = 0.81$ for *P. kofoidii*; $r = -0.13$, $P = 0.79$ for *A. mediterraneum*). However, the highest mean BL per cell of *N. scintillans*, *P. kofoidii*, and *A. mediterraneum* was achieved at a salinity of 40, at which the positive growth rates were lowest. The lowest mean BL per cell of *N. scintillans*, *P. kofoidii*, and *A. mediterraneum* was achieved at the lowest salinity tested, at which the growth rates were negative.

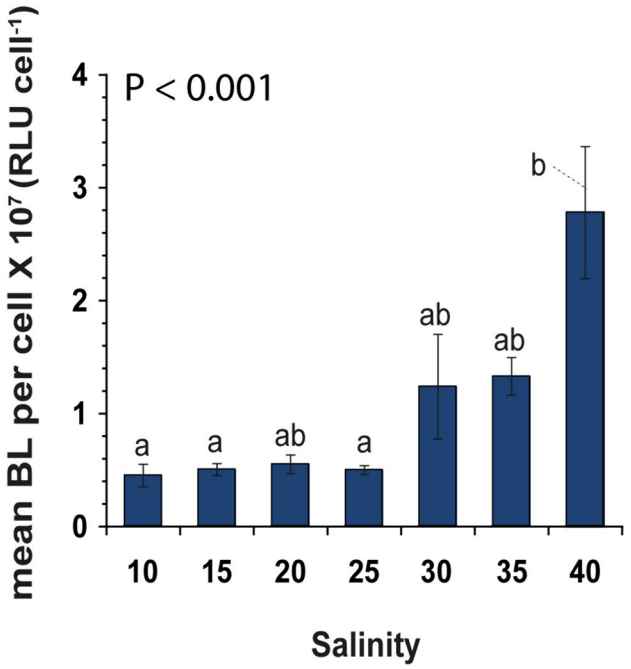


Fig. 5 Bar graph of mean 200-s-integrated bioluminescence intensity (BL) per cell of *Noctiluca scintillans* feeding on *Dunaliella salina* as a function of salinity at 10–40. Mann–Whitney U test with Bonferroni correction after the Kruskal–Wallis test resulted in significantly different subsets for the mean BL per cell (a; $P < 0.05$). Different letters on the top of the bars indicate a significant difference between the subsets. Bars represent treatment mean values ± standard error (n = 5)

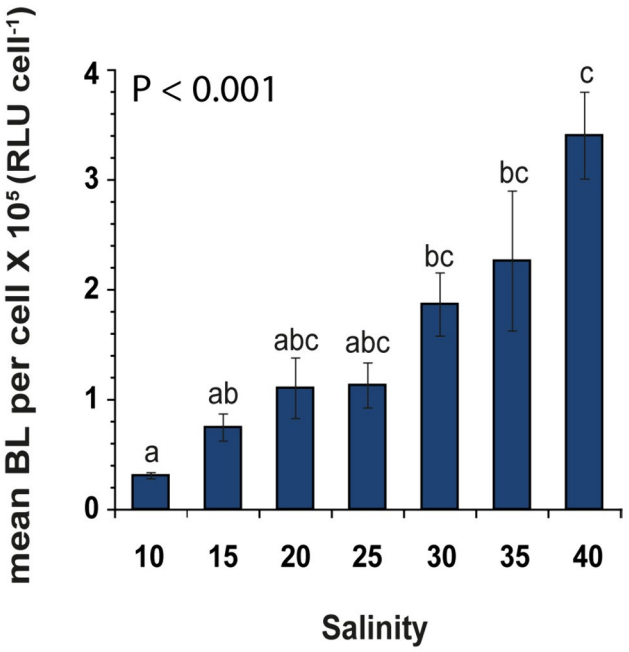


Fig. 6 Bar graph of mean 200-s-integrated bioluminescence intensity (BL) per cell of *Polykrikos kofoidii* feeding on *Alexandrium minutum* as a function of salinity at 10–40. Mann–Whitney U test with Bonferroni correction after the Kruskal–Wallis test resulted in significantly different subsets for the mean BL per cell (a; $P < 0.05$). Different letters on the top of the bars indicate a significant difference among the subsets. Bars represent treatment mean values ± standard error (n = 5)

Correlations between the cell volume and bioluminescence intensity of three dinoflagellates

When the BL per cell values of *N. scintillans*, *P. kofoidii*, and *A. mediterraneum* were pooled at a salinity of 25, log (BL per cell) showed a significant positive correlation with log (cell volume) (Fig. 9; Spearman's rank correlation; $rs = 0.95$, $P < 0.01$). Similar patterns were observed at salinities of 30, 35, and 40 (Spearman's rank correlation; $rs = 0.95$, $P < 0.01$ for salinity 30; $rs = 0.95$, $P < 0.01$ for salinity 35; $rs = 0.95$, $P < 0.01$ for salinity 40).

Discussion

To the best of our knowledge, this is the first study to explore the effects of salinity on the bioluminescence intensity of the heterotrophic dinoflagellates *N. scintillans* NSDJ2010, *P. kofoidii* PKJH1607, and an autotrophic dinoflagellate *A. mediterraneum* AMYS1807. The results of the present study extended the number of dinoflagellates investigated for the effects of salinity on bioluminescence intensity from one to four.

Although the growth rates of *N. scintillans* were similar at salinities of 10 and 40, that is, almost zero, the cell volume of *N. scintillans* was 1.7 times larger at a salinity of 10 than at a salinity of 40. Due to osmosis, the lowest salinity is likely to cause the cells to become swollen, while the highest salinity is likely to cause the cells to shrink. Furthermore, the growth rates of *P. kofoidii* were the lowest and second lowest at salinities of 10 and 40, respectively, but the cell volume of *P. kofoidii* was 2.2 times larger at a salinity of 10 than at a salinity of 40. *N. scintillans* and *P. kofoidii* do not have theca on their cell surface (Soyer 1970; Kwok et al. 2023). Thus, osmosis may largely change the volume of naked *N. scintillans* and *P. kofoidii* cells. In estuarine waters, which have a salinity of 10, large cells of *N. scintillans* and *P. kofoidii* can be found, and in salty waters with a salinity of 40, small cells of *N. scintillans* and *P. kofoidii* can be found. However, their abundance is likely to be low under both conditions due to their low growth rate.

The mean BL per cell values of *N. scintillans*, *P. kofoidii*, and *A. mediterraneum* were lowest at the lowest salinity tested, even though the cell volumes were largest. Considering their zero or negative growth rates, the cells found at these lowest salinities were likely to be almost dead and their bioluminescence became dim. On the contrary, the

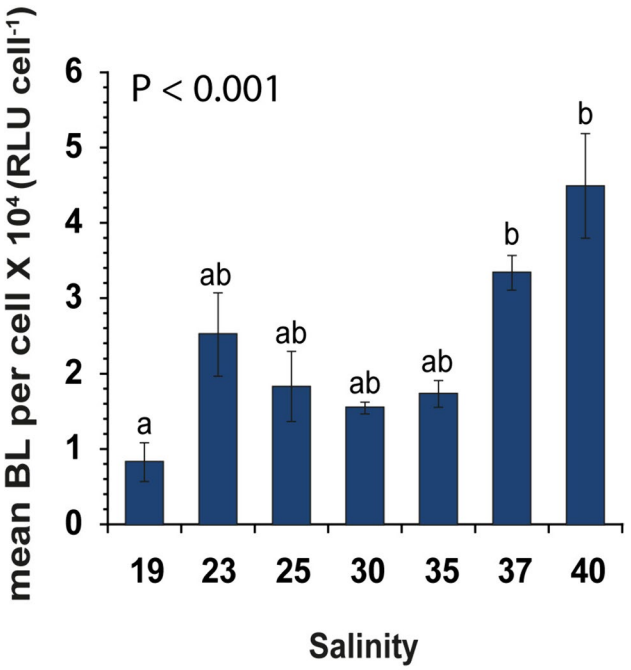


Fig. 7 Bar graphs of mean 200-s-integrated bioluminescence intensity (BL) per cell of *Alexandrium mediterraneum* as a function of salinity at 19–40. Mann–Whitney U test with Bonferroni correction after the Kruskal–Wallis test resulted in significantly different subsets for the mean BL per cell (a; $P < 0.05$). Different letters on the top of the bars indicate a significant difference between the subsets. Bars represent treatment mean values ± standard error ($n = 5$)

mean BL per cell values of *N. scintillans*, *P. kofoidii*, and *A. mediterraneum* were highest at the highest salinity, even though their cell volumes were small and their growth rates were low.

Craig et al. (2003) also showed that the bioluminescence intensity of *Pyrocystis lunula* was the lowest at a salinity of 17 and highest at a salinity of 38 when the tested salinity range was 17–48 (Table 3). The bioluminescence intensities of *P. lunula* at salinities of 43 and 48 were slightly lower than those at salinities of 38. Therefore, the results of Craig et al. (2003) and our experiments clearly show that the bioluminescence intensity of dinoflagellates is high at high salinity and low at low salinity if the cells survive.

At salinities higher or lower than the isosmotic point, the intracellular ion concentration is altered by osmoregulation or osmoadaptation (Wegmann 1986; Kirst 1990; Mayfield and Gates 2007; Suescún-Bolívar and Thomé 2015). Increasing extracellular salinity increases cytosolic Ca^{2+} and K^+ in various organisms (Dickson and Kirst 1987a, b; Lynch and Läuchli 1988; Lynch et al. 1989; Lee and Liu 1999; Laohavisit et al. 2013; Seifikalhor et al. 2019); it also increases the accumulation of intracellular K^+ inside phytoplankton cells (e.g. Dickson and Kirst 1987a, b). The concentrations of Na^+, K^+, Ca^{2+}, and Mg^{2+} in the cytosol of *N. scintillans* can be altered by water efflux and influx into cells (Nawata and Sibaoka 1976). During bioluminescence in dinoflagellates, Ca^{2+} is released from intracellular Ca stores or absorbed from extracellular sources, which increases the Ca^{2+} concentration inside the cytosol and triggers bioluminescence (Haley et al. 1995; Lumpkin and Hudspeth 1995; von Dassow and Latz 2002). Von Dassow and Latz (2002) reported that the bioluminescence of *Lingulodinium polyedra* was stimulated by an increase in extracellular Ca^{2+} and K^+. Thus, increased salinity may lead to increased ion concentrations in the extracellular environment (Dittmar 1884; Forchhammer 1865; Trask 1936), which can enhance the influx of Ca^{2+} and K^+ into the cytosol and ultimately increase bioluminescence. In the present study, deionized water and sea salt were used to achieve the target salinities. Therefore, there are potential discrepancies associated with the means of dilution and the concentration of seawater in natural marine environments.

The range of salinities in global oceans, except for extreme cases of high salinity, is 0.5 – 42 (Brewer and Dyrssen 1985; John et al. 1990; Samuelsson 1996; Matthäus and Schinke 1999; Talley 2002; Emeis et al. 2003; Meier and Kauker 2003; Feistel et al. 2010; Urquhart et al. 2012). The range of salinities at which cells have been observed is 10 – 39 for *N. scintillans*, 8 – 38 for *P. kofoidii*, and 17 – 37 for *A. mediterraneum* (Buskey et al. 1992; Elbrächter and Qi 1998; Gómez 2003; John et al. 2003; Mohamed and Mesaad 2007; Lilly et al. 2007; Penna et al. 2008; Aguilera-Belmonte et al. 2011; Harrison et al. 2011; Chuenniyom et al. 2012; Ocean Survey 20/20 2013; Tillmann and Hoppenrath 2013; Yoo et al. 2013; Giulietti 2017; Lim et al. 2017; Prabowo and Agusti 2019; Eom et al. 2021; Park et al. 2021; Ok et al. 2023). The range of BL per cell values of *N. scintillans* in global oceans is expected to be 0.45×10^7 to 2.78×10^7 RLU $cell^{-1}$, a sixfold difference between cells at the upper and lower ends of the range. The range of BL per cell values of *P. kofoidii* in global oceans is expected to be 0.31×10^5 to 3.40×10^5 RLU $cell^{-1}$, which is an 11-fold difference. The range of BL per cell values of *A. mediterraneum* in global oceans is expected to be 0.83×10^4 to 3.34×10^4 RLU $cell^{-1}$, which is a fourfold difference. Thus, when considering the effects of salinity, the difference in the BL per cell values in global oceans is likely to be larger among *P. kofoidii* cells than among *N. scintillans* or *A. mediterraneum* cells.

The bright bioluminescence of dinoflagellates is known to startle predatory copepods or draw the attention of higher-order predators to the copepod's location (White 1979; Esaias and Curl 1972; Prevett et al. 2019). Various genera of dinoflagellates, except for *N. scintillans* and *P. kofoidii*, show mechanisms for inhibiting the stimulation of bioluminescence in the presence of light (Hamman et al. 1981a, b; Sweeney et al. 1983; Sullivan and Swift 1994; Buskey et al. 1992; Li et al. 1996). Consequently,

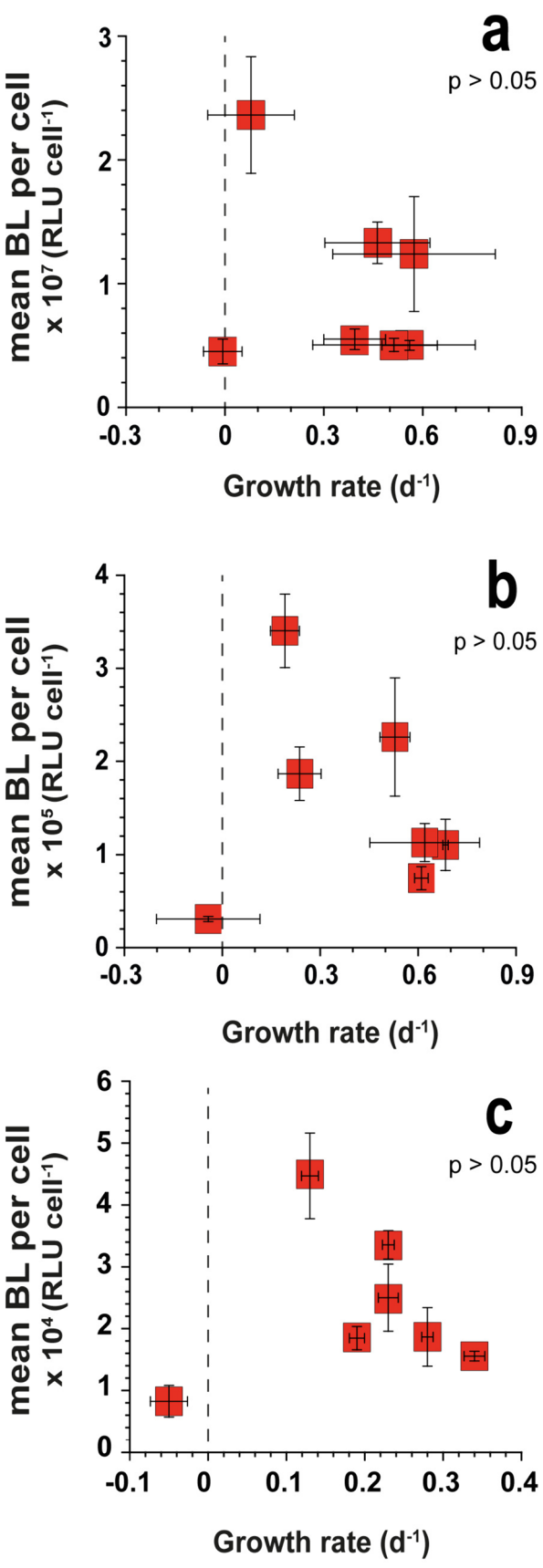


Fig. 8 The mean 200-s-integrated bioluminescence intensity (BL) per cell of *Noctiluca scintillans* feeding on *Dunaliella salina* (**a**) and *Polykrikos kofoidii* feeding on *Alexandrium minutum* (**b**) and *Alexandrium mediterraneum* (**c**) as a function of the growth rate of *N. scintillans*, *P. kofoidii*, and *A. mediterraneum*, respectively

grazing deterrence by *A. mediterraneum* using its luminescence occurs primarily at night, while *N. scintillans* and *P. kofoidii* can be effective both at night and when ambient light is dim. The mean BL per cell values of *N. scintillans*, *P. kofoidii*, and *A. mediterraneum* are greater at high salinities, which are usually found in offshore and oceanic waters, than at low salinities, which are usually found in estuarine waters. Therefore, in offshore and oceanic waters, the bright bioluminescence of dinoflagellates will likely reduce predation by copepods. However, in estuarine waters, the dim bioluminescence of dinoflagellates may not reduce predation by copepods. Furthermore, high turbidity in estuarine waters may mask the bioluminescence of dinoflagellates, which may not affect predation by copepods.

During World War I, a German U-boat was discovered and sunk due to bioluminescence in the Strait of Gibraltar (Fernandes and Bajaj 2022). Bioluminescence produced by marine organisms has been studied by some countries to detect warships and submarines at night (Lynch 1978, 1981; Lapota 2003, 2005; Moline et al. 2005). Warships operate in most marine countries and submarines operate in several countries, such as the United States, the United Kingdom, South Korea, China, and Russia (Global Firepower 2023). Warships and submarines travel from their bases to oceans worldwide to carry out operations, and they encounter a diverse range of salinity levels (Pritchard 1952; Lundeberg 1963; Charette and Buesseler 2004; Feistel et al. 2010). During the daytime, the movement of submarines is tracked using information obtained by military reconnaissance satellites (Chriqui 2006; Shabbir et al. 2019). However, it is difficult to acquire this information at night and thus, bioluminescence stimulated by operating submarines can be used for detection (Moline et al. 2005). The Strait of Gibraltar connects the Atlantic Ocean and the Mediterranean Sea, and has a salinity range of 35 to 38 (Bryden et al. 1994; Flecha et al. 2019). Blooms of *N. scintillans* and *P. kofoidii* have been reported in the Atlantic Ocean and the Mediterranean Sea (Harrison et al. 2011; Provoost and Enevoldsen 2023). Based on the results of the present study, blooms of *N. scintillans* and *P. kofoidii* would produce close to their brightest bioluminescence at these high salinities and the waves generated by moving warships and submarines are likely to stimulate these dinoflagellates to produce bright bioluminescence, which can be easily detected.

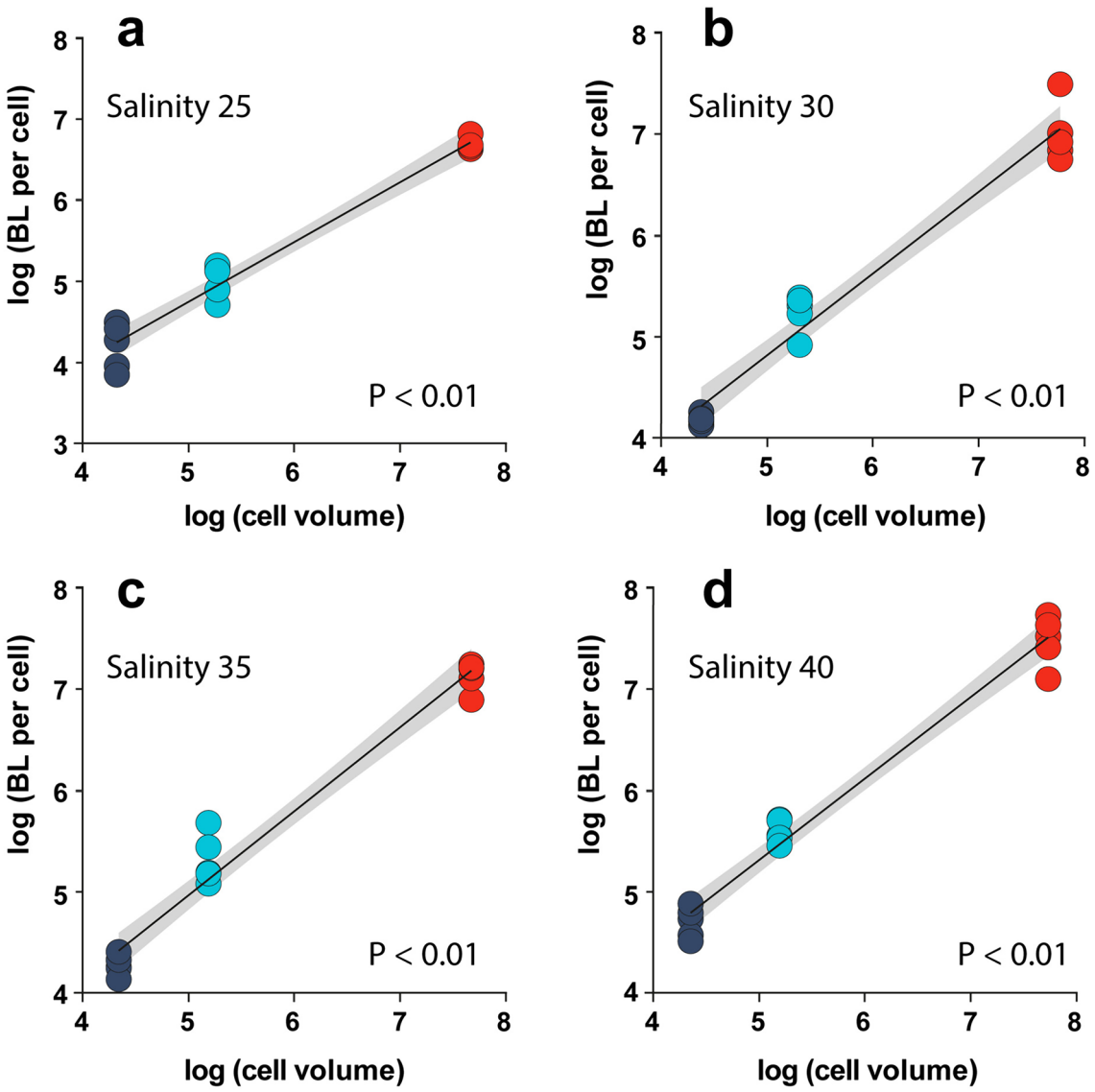


Fig. 9 The logarithm of 200-s-integrated bioluminescence intensity (BL) per cell as a function of the logarithm of the cell volume of *Noctiluca scintillans* (red circle), *Polykrikos kofoidii* (blue circle), and *Alexandrium mediterraneum* (green circle) at a salinity of 25 (**a**), 30 (**b**), 35 (**c**), and 40 (**d**). The regression line, indicated by the black line, represented the corresponding equation and the shaded areas represent the 95% confidence interval. The equations of linear regression: **a** log (BL per cell) = 0.74 log (cell volume) + 1.06, $r^2 = 0.97$ ($P < 0.01$); **b** log (BL per cell) = 0.81 log (cell volume) + 0.79, $r^2 = 0.96$ ($P < 0.01$); **c** log (BL per cell) = 0.83 log (cell volume) + 0.83, $r^2 = 0.97$ ($P < 0.01$); **d** log (BL per cell) = 0.80 log (cell volume) + 1.23, $r^2 = 0.98$ ($P < 0.01$). Symbols represent single treatment

Table 3 Effect of salinity on the bioluminescence intensity of bioluminescent dinoflagellates

Bioluminescence species		Salinity range	S–BL	Ref
Dinoflagellate	*Noctiluca scintillans*	10–40	+	This study
	Polykrikos kofoidii	10–40	+	This study
	Alexandrium mediterraneum	19–40	+	This study
	Pyrocystis lunula	17–38[a]	+	Craig et al. (2003)
		38–48[a]	−	Craig et al. (2003)

S–BL, relationship between salinity and bioluminescence intensity; +, positive relationship; −, negative relationship

[a]not acclimated the culture to the salinity

The U.S. Norfolk Naval Base, currently the world's largest naval facility, is located in Chesapeake Bay (Conger 2019). Inflow from the Elizabeth River affects the salinity in this area, which is less than 16 (Pritchard 1952; Charette and Buesseler 2004; Urquhart et al. 2012). Furthermore, the area exhibits consistently high turbidity throughout the year, which is attributed to the inflow of suspended particulate matter (Shuyler et al. 1995). Considering the scattered and reduced bioluminescence due to turbidity and salinity, detecting bioluminescence stimulated by submarines or ships within the base may be challenging.

In the present study, *N. scintillans* showed almost zero growth at the lowest salinity tested, potentially resulting in similar mean BL per cell values for the lowest salinity and salinities of 15–25. Meanwhile, negative growth rates were observed for *P. kofoidii* and *A. mediterraneum* at the lowest salinity, indicating sublethal salinity stress. Under this condition, *P. kofoidii*, and *A. mediterraneum* showed the lowest mean BL per cell. A reduction in the bioluminescence of dinoflagellates is also observed when they are exposed to various sublethal stressors, such as heavy metals, ammonia, polycyclic aromatic hydrocarbons, and sediment-bound metals and organic compounds (Hannan et al. 1986; Lapota et al. 1993, 1995, 1997, 2007; Lapota 1998; Okamoto et al. 1999; Rosen et al. 2008; Hildenbrand et al. 2015; Perin et al. 2022). Consequently, the findings of our study suggest that salinity can serve as an indicator of sublethal stress, leading to a reduction in dinoflagellate bioluminescence.

The rates of inhibition of dinoflagellate bioluminescence, used to assess acute and sublethal toxic effects, have been investigated under exposure to a toxicant for durations ranging from 2 h to 11 days (Hannan et al. 1986; Lapota et al. 1993; Craig et al 2003; Rosen et al. 2008; Stauber et al. 2008; Hildenbrand et al. 2015; Perin et al. 2022). In the present study, the duration of acclimation to the target salinity ranged from 9 to 14 days, and Craig et al. (2003) had a duration of 4 h. In these investigations, the bioluminescence of dinoflagellates was significantly affected by salinity. Changes in salinity significantly had a notable impact on the inhibition of bioluminescence in *P. lunula* induced by sodium dodecyl sulfate (Craig et al. 2003). Therefore, salinity should be carefully considered when performing bioassays, as it can affect the rate of inhibition of bioluminescence. The findings of the present study provide a basis for understanding the impact of environmental factors on dinoflagellate bioluminescence and may further contribute to our understanding of the function of dinoflagellate bioluminescence in the marine planktonic food web and application of bioluminescence.

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Authors contribution SAP and HJJ designed the study conception and drafted the manuscript. SAP, JHO, HCK, JHY, SHE, MJL and YYD conducted experiments including bioluminescence intensities and growth rates measurement. SAP, JHO and HJJ conducted data analyses. All authors discussed the results.

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Data availability Enquiries about data availability should be directed to the authors.

Declarations

Conflict of interest The authors declare that they have no competing interests.

Ethical approval All applicable international, national, and institutional guidelines for sampling, care, and experimental use of organisms for the study have been followed.

Consent to participate Not applicable.

Consent to publish All authors consent to the publication of this manuscript.

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